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K^+, Osmoregulation and Drought Tolerance - An Overview

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Osmoregulation is an important adaptive mechanism in higher plants enabling turgor maintenance under drought environments. In prokaryotes like *E. coli* potassium accumulation is the initial primary response to reduced osmotic pressure in the external environment with reduction in turgor pressure serving as the triggering agent. The accumulation of another compatible solute like betaine is induced by an operon of three genes kdpABC which is regulated by the product of kdpD gene, a membrane protein. In crop plants also, genotypic differences in osmoregulation in wheat are controlled by a single locus with high osmoregulation being recessive. K^+ accumulation could largely account for high osmoregulation with amino acids being another important contributor. Preliminary results indicate similar trends in chickpea cultivars. However, K^+ spray during post anthesis phase did not significantly affect the response to drought in wheat cultivars and species.

Key Words: Potassium, Osmoregulation, Drought

Introduction

Osmotic adjustment involves the active accumulation of solutes in response to drought which leads to lowering of osmotic potential, consequently maintaining cell turgor at lower soil water potential and enhancing various turgor-dependent processes (Khanna-Chopra & Sinha 1991). The term is derived from the concept of osmoregulation observed in microorganisms whereby they adapt to the changes in solute concentrations in external environment by regulating osmotic pressure, thereby regulating turgor and growth (Sutherland et al. 1986). In higher plants growth is often more sensitive to water deficit than photosynthesis, hence slowing of growth may lead to accumulation of some solutes and osmotic adjustment. In addition there is active accumulation of amino acids and specifically proline and betaine in some plants (Paleg & Aspinall 1981). Proline accumulation has been shown to be due to enhanced biosynthesis and slow degradation of proline in water stressed plants.

Osmolytes and Osmotic Adjustment

The major solutes contributing to osmotic potential include common metabolites such as sugars, amino acids, organic acids and ions such as nitrate, chloride and potassium (Morgan 1984). The response of expanded and expanding wheat leaves subjected to water stress are different in terms of relative changes in various solutes contributing to osmotic potential. In expanding leaves initial changes in osmotic potential were largely due to reducing sugars while amino acids became significant later coinciding with the loss of turgor (Munns et al. 1979). In expanded leaves, changes in potassium, sugars and amino acids accounted for most of the changes in os-

motic potential. The changes in sugars mainly involved sucrose, glucose and fructose while proline and aspargine accounted for amino acid accumulation. Morgan (1991) coined the term osmoregulation for that component of osmotic adjustment which contributes to the maintenance of turgor. Genotypic differences in osmoregulation in wheat varieties were linked to alternative alleles at a single locus with high osmoregulation being recessive. Analysis of osmotic components in wheat lines showing high and low osmoregulation revealed major differences in accumulation of K^+ followed by amino acids (table 1). Sugar accumulation was not found. K^+ accumulation in response to water stress in high osmoregulating wheat lines led to maintenance of turgor. This response was quite similar to that of *E. coli* wherein K^+ accumulation was the primary response to a reduction in external osmotic pressure which subsequently leads to betaine accumulation. Stress induced potassium accumulation in *E. coli* involves an operon of three genes, KdpABC which is regulated positively by the product of KdpD gene, a membrane bound protein that acts as a turgor pressure sensor (Sutherland et al. 1986). The genes responsible for osmoregulation in mesophytes need to be identified and their regulation studied in detail in order to understand the evolution of stress response.

K^+ and Drought Stress

Drought stress affects plant growth through reduced availability of water. Roots are the primary organs to sense the reduction in available water in soil and convey the message to shoot wherein a number of responses occur such as stomatal closure, reduced growth, etc. Although turgor responsive genes are being identified, the proteins they code for are not known.

Studies on osmotic adjustment in crop plants have been done mostly during vegetative stage in pot grown plants. Does a plant showing high osmoregulation capacity during vegetative stage retain this response during grain development? Since osmotic adjustment involves partitioning of photosynthates and accumulation of ions it may be influenced by the strength of reproductive sink. Thus, a plant showing high yield potential may show capacity for low osmotic adjustment compared to a plant with low yield potential. Similarly, ions accumulation in a water-stressed tissue can occur only till ion-uptake processes are not influenced by drought stress.

We analysed the osmotic components of leaves of wheat and chickpea varieties (desi and kabuli) under water stress during reproductive phase. Leaves having flowers in their axil in chickpea and flag leaf in wheat were chosen for the study. Cell sap was extracted after freezing

Table 1 *Relative contributions by major solutes to osmotic potential for wheat lines with high and low osmoregulation near full and near zero turgor, together with standard errors (Morgan 1992)*

	Potassium	Total amino acids	Sugars
		(-MPa)	
Low osmoregulation group			
Full turgor	0.522±0.031	0.382±0.036	0.108±0.009
Zero turgor	0.498±0.021	0.424±0.025	0.085±0.006
High osmoregulation group			
Full turgor	0.443±0.020	0.408±0.030	0.113±0.017
Zero turgor	0.524±0.020	0.385±0.028	0.070±0.006

and thawing of leaves and analysed for amino acids, sugars, proline and K^+ ion content at various stages of pod/seed development. At flowering stage chickpea leaves in water stressed plants accumulated K^+ and amino acids more than sugars in response to decrease in water potential and solute potential (figure 1). Thus K^+ ions were the major contributors towards osmotic adjustment in chickpea leaves. These results are similar to those observed by Morgan (1992). However, during mid pod development stage as the intensity of water stress increased K^+ ion accumulation was considerably reduced (table 2). In fact in some chickpea varieties (Kabuli BG 1001) K^+ content in leaves did not increase in response to stress. Sugars, amino acids, proline and K^+ could only account for 61-75% of the osmotic potential of cell sap in irrigated or water stressed leaves. This is the first report on the nature of metabolites contributing to osmotic potential in chickpea leaves. These results indicate varietal differences in sensitivity of ion uptake processes to water stress. Similar results have been obtained in other crops also (Tanguilig et al. 1987).

Studies on flag leaf of wheat from irrigated and stressed plants of *T. aestivum* var. Kalyansona, C306 and *T. polonicum* revealed interesting results (tables 3, 4). Kalyansona, a high yielding variety, showed accumulation of amino acids and proline in

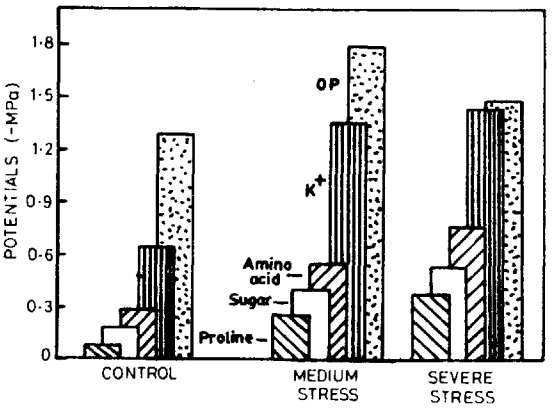

Figure 1 Osmotic constituents of chickpea leaves from irrigated and water stressed plants

response to water stress while sugars and ions did not accumulate. In contrast *T. polonicum*, having an average yield, exhibited accumulation of sugars, amino acids, proline and ions as solute potential declined. The decline in osmotic potential with increase in stress intensity was also more in *T. polonicum* compared to Kalyansona and C306. These results reveal an interesting relationship between "sink strength" and the capacity for osmotic adjustment. In fact in barley, isolines showing high capacity for osmotic adjustment were associated with low grain yields (Grumet et al, 1987). This observation needs further analysis.

Table 2 *Solutes and K^+ contributing to osmotic potential in cell sap of desi and kabuli chickpea leaves during mid pod development stage*

Water potential	Osmotic potential (OP)	Sugars	Amino acids	Proline	K^+ Content	OP accounted for
			(-MPa)			
PUSA 256 (Desi)						
1.13	1.44	0.10	0.17	0.09	0.67	1.03
2.17	1.96	0.10	0.20	0.34	0.84	1.48
BG 1001 (Kabuli)						
1.73	2.37	0.20	0.39	0.15	0.77	1.51
2.07	2.52	0.16	0.37	0.32	0.69	1.54

Table 3 *Solute content in flag leaf of wheat varieties and species during grain development in irrigated and drought stressed plants*

Genotype Treatment	Solute potential (-MPa)	Sugars mg(gDW)-1	Amino Acids m mole (gDW)-1	Proline m mole(gDW)-1	DAA
Kalyansona					
Control	-2.3	90.0±2.8	152.0±5.7	3.6±0.07	15
Stress	-2.8	93.8±1.3	174.5±19.0	30.1±1.47	
C306					
Control	-2.3	98.1±1.3	91.3±4.14	6.1±0.29	10
Stress	-2.9	84.6±1.9	86.0±3.4	34.7±0.5	
T. Polonicum					
Control	-2.7	78.8±4.0	132.1±6.47	5.2±0.66	5
Stress I	-2.9	74.0±1.1	125.5±6.17	22.9±1.43	
Stress II	-3.3	94.5±2.55	179.6±5.0	42.9±0.5	
Stress III	-3.5	95.2±2.27	195.3±11.1	68.8±1.27	
T. Polonicum					
Control	-3.5	53.2±0.84	63.1±6.1	31.3±0.74	12
Stress I	-4.0	63.0±1.45	108.1±7.2	51.5±1.1	
Stress II	-4.4	67.0±0.5	110.5±4.52	54.8±0.93	
Stress III	-4.8	71.6±1.55	183.8±13.42	109.2±1.56	

Table 4 *Ion content in flag leaf of wheat varieties and species during grain development in irrigated and drought stressed plants*

Genotype Treatment	Solute potential (-MPa)	*Ions mg (g DW)*$^{-1}$ K+	Na+	Ca^{++}	Mg^{++}	DAA
Kalyansona						
Control	-2.3	10.1±0.08	0.4±0.01	3.8±0.01	4.7±0.22	15
Stress	-2.8	9.2±0.07	0.6±0.05	4.2±0.01	5.0±0.12	
C306						
Control	-2.3	8.8±0.05	0.5±0.02	5.8±0.18	6.7±0.41	10
Stress	-2.9	11.7±0.2	0.6±0.02	6.4±0.19	9.0±0.84	
T. polonicum						
Control	-2.7	16.2±1.33	1.9±0.02	5.9±0.32	1.7±0.3	5
Stress I	-2.9	11.1±0.32	2.7±0.04	6.5±0.01	2.8±0.25	
Stress II	-3.3	9.3±0.25	3.4±0.02	7.3±0.01	2.2±0.05	
Stress III	3.5	15.0±0.8	2.2±0.13	6.5±0.01	2.7±0.2	
T. polonicum						
Control	-3.5	11.2±0.5	2.6±0.05	5.9±0.2	2.0±0.2	12
Stress I	-4.0	9.8±2.1	2.9±0.1	6.5±0.01	2.2±0.08	
Stress II	-4.4	7.6±0.04	3.0±0.14	6.5±0.01	2.6±0.06	
Stress III	-4.8	15.8±2.4	2.4±0.08	6.0±0.0	2.3±0.23	

Days after anthesis (DAA). Stresses I, II, III refer to mild stress, medium stress and severe stress respectively.

K^+ ions are known to be beneficial under drought stress through their effects on leaf osmotic potential, turgor potential, cell size and leaf water content (Jensen et al. 1982). K^+ fertilized plants exhibited higher WUE, dry matter accumulation and grain yield in drought stress environments (Jensen & Tophoj 1985). Can these beneficial effects of K^+ be induced by K^+ spray in plants subjected to different intensities of water stress? Wheat varieties Kalyansona and C306 and *T. sphaerococcum* plants were sprayed with 0.2M solution of potassium nitrate at 46, 70, 88 and 109 days after sowing. The leaves were analysed for metabolites such as amino acids, sugars, proline and ions. Grain yield and biomass were also recorded. K^+ application increased grain yield in Kalyansona at all levels of available water (figure 2). There was no effect on grain yield of C306 and *T. sphaerococcum*. This response could not be related to leaf water relations as K^+ application had no consistent effect on solute potential of leaves. However, it is speculated that K^+ spray might have stimulated root growth (Khanna-Chopra et al. 1980) and hence facilitated water and nutrient uptake resulting in increased grain yield. Kalyansona being a high-yielding variety responded better than C306 and *T. polonicum*.

Osmotic Adjustment and Yield Stability

Osmotic adjustment is an inducible character and is considerably influenced by the environment (Ludlow & Muchow 1988). Crop plants experience water deficit varying in intensity and duration during growth and development. Can osmotic adjustment help in maintaining growth and physiological processes in water limited environments and thus stabilize crop productivity? This aspect was examined in wheat varieties and species, varying in yield potential, by growing in water variable environments and measuring osmotic adjustment in the flag leaf in the flowering and post flowering period. Considerable variation was observed in the

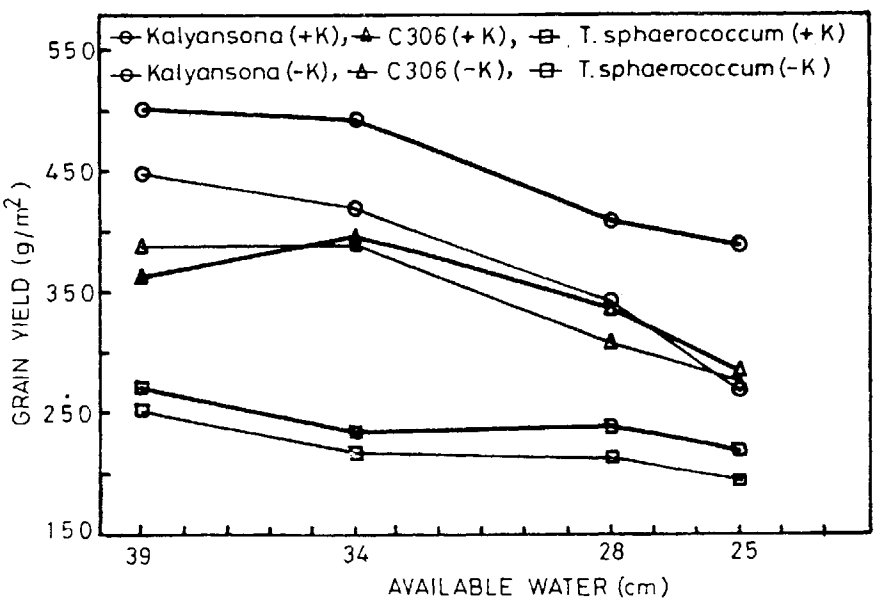

Figure 2 Effect of K^+ application on grain yield of wheat varieties and species grown with different levels of available water

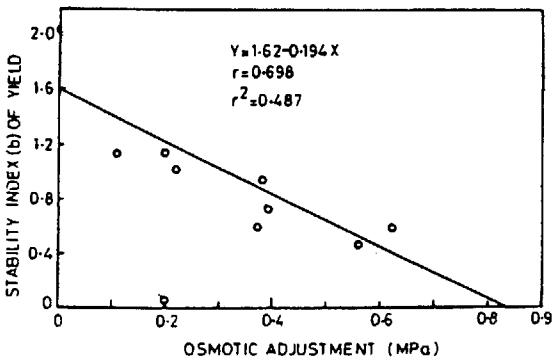

Figure 3 Relationship between osmotic adjustment and stability index for grain yield in wheat varieties and species. *T. aestivum* varieties Kalyansona, C306, Banks, Cook, Kite, Harrier, Millewa, *T. sphaerococcum* and *T. polonicum*

capacity for osmotic adjustment in wheat lines during the post flowering phase. High osmoregulating lines showed higher stability for grain yield (figure 3), biomass and grain number. These results confirmed the earlier reports in wheat, sorghum and chickpea wherein yield increases have been obtained by selecting for high osmotic adjustment (Morgan 1983, Santamaria et al.1990). Yield stability in stress environments is often associated with low yields (Sinha et al. 1986). Hence, a threshold of stability and productivity need to be worked out in different environments. Osmotic adjustment can be a criterion of yield stability and hence of drought tolerance but is associated with low yield.

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